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A New Adaptive Landscape: Urbanization as a Strong Evolutionary Force

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To the Graduate Council:

I am submitting herewith a thesis written by Lauren Christie Breza entitled "A New Adaptive Landscape: Urbanization as a Strong Evolutionary Force." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

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A New Adaptive Landscape: Urbanization as a Strong Evolutionary Force

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ABSTRACT

Urbanization is rapidly increasing as human population growth steadily grows, but there is little consensus of the ecological consequence of this population shift and almost no information of the evolutionary consequences for local biodiversity. Nearly two-thirds of the world's population will live in city centers by 2050 with profound impacts on landscapes that can act as important agents of selection. This study aims to identify 1) the net effect of urbanization on species richness, 2) how phylogenetic diversity varies between urban and rural sites, and 3) the strength of urbanization as a selection pressure. First, a meta-analysis was conducted in order to calculate an overall effect size that reflects differences in species richness in urban versus rural sites. Then a subset of the data was used to calculate phylogenetic species variance (PSV), phylogenetic species richness (PSR), and species richness (SR) of plants within urban and rural sites. Lastly, a SURFACE analysis, using a combined phylogeny of the species surveyed, was used to detect regime shifts and quantify the strength of selection. These results show: 1) species richness is significantly lower in urban ecosystems than and rural; 2) no difference in PSV, PSR, and SR between urban and rural ecosystems; but 3) there was a strong phylogenetic signal for plant responses to urbanization. The results of this study indicate that urbanization is selecting novel communities based on highly conserved functional traits. As global populations continue to grow, urbanization will continue to be a strong force of natural selection and urban centers may become a new evolutionary landscape with novel conservation strategies required to preserve associated biodiversity.

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CHAPTER 1
INTRODUCTION

Urbanization is a strong anthropogenic force that directly contributes to habitat destruction and fragmentation, which are the leading causes of biodiversity loss worldwide (Fahrig 2003; Pimm 2008). The rate of urbanization accelerated over the last century and is expected to continue at an annual rate of 1.7% between now and 2030 with over two-thirds of the word's population living within urban centers by the year 2050 (United Nations 2015a). The impact of urbanization on biodiversity will consequently become even stronger as ecosystems transition from their natural states to urbanized states (United Nations 2015b). As of 2010, the global urban land was approximately 350 million hectares, developed land was 71 million ha, and impervious surfaces was 59 million ha, covering almost 4% of the Earth's total land area (Liu *et al.* 2014). In addition, the amount of agricultural land needed to support both urban centers and rural communities contributes an additional 33% of the Earth's total land area (Alexandratos & Bruinsma 2012). The industrialization of natural ecosystems results in a reduction in available habitat and will likely be devastating for species across broad taxonomical groups, with many already being at risk for extinction under the current levels of urbanization.

Recent literature reviews indicate that in most cases, urbanization decreases biodiversity with the potential to alter community composition (McKinney 2006, 2008) and ecosystem function (McDonnell *et al.* 1997; Alberti 2005; Kaye *et al.* 2006). For example, Newbold (2015) found that with intensifying global land use change there is a sharp decline in species richness. From a conservation standpoint, this information is critical to how we plan cities in the future. However, there is still little information on how urbanization may act as selective force and impact evolutionary processes. Urban ecosystems are novel in that they have higher levels of CO2 (Pataki *et al.* 2006), warmer temperatures(McDonnell *et al.* 1993; Pickett *et al.* 2008), drier conditions (Paul

& Meyer 2001), and higher levels of pollution deposits (Vitousek *et al.* 1997). Because of the novelty of these niches, urban ecosystems have the potential to select for particular suites of species with phenotypes that are capable of withstanding such harsh environments (Williams *et al.* 2009). Incorporating phylogenetics into ecological studies is one approach to determine whether the effects of urbanization are due to evolutionary history or external abiotic forces. Taking a phylogenetic perspective also offers insight into the way evolutionary relationships shape present day community assemblages (Webb *et al.* 2002; Cavender- Bares *et al.* 2009).

This study took a two-part approach to understand the evolutionary impacts of urbanization on species diversity: 1) A meta-analysis was used to determine if urbanization decreases species richness; based on current knowledge, it was hypothesized that urban ecosystems have fewer species than rural ecosystems. 2) A series of phylogenetic analyses was conducted on a subset of the data to determine how evolutionary history is related to species response to urbanization and quantify the strength of urbanization as a selection pressure. It was hypothesized that urbanization is a strong evolutionary force, selecting for particular groups of species that can tolerate urban habitats. Consistent with these predictions, these results show that urbanization is among the most powerful selective forces quantified resulting in a loss of biodiversity, no differences in phylogenetic diversity, but unique and related groups of species in urban centers relative to rural ecosystems based on highly conserved functional traits.

CHAPTER 2
METHODS

Data Collection

The Web of Science Database (v5.15; Thompson Reuters, ISI Web of Knowledge) was searched for relevant studies between 1990 and 2015 with the following search terms: “Urban” or “Urbanization” or “Urban-Rural” AND “Species Diversity” or “Species Richness” or “Biodiversity” AND “Plant” or “Animal”. The preliminary search yielded approximately 19,000 studies and was refined by Research Domains, Research Areas, and by Document types resulting in 15,843 publications. The literature search was further narrowed by searching for “Shannon” OR “Simpson” within the results, yielding 296 studies. The literature search was refined once more by determining relevance from titles and abstracts resulting in a pool of 47 studies; 23 studies who’s target taxa were plants, 23 studies who’s target taxa were animals, and one study that focused on both plant and animal diversity. All publications used for data extraction were: 1) published in a peer reviewed journal; 2) consisted of primary data; 3) the response variable included but was not limited to species richness; 4) used at least one urban and one rural study sites. Studies were removed from the pool if species richness data were not available.

From the above studies, data for city size, city latitude and city longitude, Human Development Index, Kingdom (plant or animal), growth type (woody/herbaceous, invertebrate/vertebrate), and response variables defined by an index of species diversity for rural and urban study sites (richness, Shannon-Weiner, and Simpson’s index of diversity) were extracted. Plot Digitizer was used (Plot Digitizer, version 2.6.6) to extract data points from figures if the information was not readily available in table format. If the study collected species abundance data, but species diversity statistics were not reported (nearly half of all studies used), then authors were contacted to gain permission to use and access the data or data published in supplemental appendices were used. In either case, the R package vegetarian (Charney & Record 2013) was

used to calculate species richness, Shannon-Weiner Reciprocal index of diversity, and Simpsons index of diversity with the raw data for urban and rural sites.

Urban and rural sites were classified using site descriptions from each study. Sites classified as “Rural” must fall outside of the city perimeter and consist of mostly natural habitat. Sites classified as “Natural” in certain studies were included in the “Rural” classification for this meta-analysis. Urban sites were less ambiguous, as they were always located in the city center and urban green spaces were classified as “Urban”. The formula for Hedges’ *d* was used to calculate effect sizes for each study by using the R package Metafor (Viechtbauer 2010). The Hedges’ *d*, or standardized mean difference (SMD), is the difference of means divided by the pooled standard deviation of the two groups. The SMD was used to calculate effect sizes because it not affected by unequal sampling variances and includes a correction factor for small sample sizes (<10 studies) (Koricheva *et al.* 2013). The SMD between urban sites and rural sites will produces a negative effect size if diversity in urban sites is lower than in rural sites, and will produces a positive effect size if diversity in urban sites is higher than rural sites.

To test how phylogenetic diversity changes on an urbanization gradient, a subset of the dataset was used to “prune” a published phylogenetic tree (Zanne *et al.* 2014) using the R packages ape (Paradis *et al.* 2004), phytools (Revell 2012), and geiger (Harmon *et al.* 2008). In total, seven studies that focused on plant taxa were used for the phylogenetic analysis due to the availability and accuracy of previously published phylogenetic trees. The criteria for this analysis required that the study provide community data consisting of species present and their abundances. Presence absence data were also accepted. The available studies for the phylogenetic analysis were reduced from the original 47 studies to a total of 17 Studies (7 plant studies, and 10 animal studies) and were further narrowed down by observing only plant species. If animals were included in the analysis, then the Tree of Life risked being skewed and the evolutionary history between species would be compromised.

The presence or absence of a species within a community (urban or rural) was used as a proxy for a suite of unknown plant functional traits. For example, there are five urban site and five rural sites and *species X* occurs in two out of five urban sites and four out of five rural sites. The proportion of *species X* occurrence in rural sites is 0.8 and the occurrence in urban sites is 0.4. The difference between rural and urban sites is 0.4; this value would then be assigned to *species X* as its strength of preference for rural or urban ecosystems. Therefore, the trait value can fall between the numbers 1 and -1. The closer the trait value is to 1, the stronger preference or success rate in rural ecosystems, if the trait value is equal to 0, there is no preference, the closer the trait value is to -1, the stronger preference or persistence rate in urban ecosystems. Under the general assumption that species presence in a particular environment is strongly linked to well-adapted functional traits, we use this proportion as a proxy for a suite of functional traits associated with high fitness (Cadotte *et al.* 2009; Adler *et al.* 2014).

Statistical Analysis

A linear mixed-effects model under restricted maximum likelihood was used to test for the net effect of urbanization on species richness (Viechtbauer 2010). Various moderators were incorporated in the analysis to determine how much study heterogeneity is explained by different factors. Kingdom and growth form were used to detect taxa level responses to urbanization. The kingdom moderator consisted of plants and animals. The growth form moderator consisted of vertebrates and invertebrates for animals and herbaceous, woody, and miscellaneous for plants, respectively. Studies that fell within the miscellaneous plant category did not provide enough information to determine which growth forms were studied. Phylogenetic Species Variability (PSV), Phylogenetic Species Richness (SPR), and overall Species Richness (SR) were calculated to determine how urbanization might be affecting phylogenetic diversity (Kembel *et al.* 2010). PSV is a measurement of the degree to which species in a community are phylogenetically related by assuming that the branch lengths of the phylogeny are proportional to the evolutionary divergence between species (Helmus *et al.* 2007). All of the species in the phylogeny are considered unrelated when PSV is

equal to one, meanwhile, as PSV approaches zero species become more related. PSR is simply the SR multiplied by the PSV. PSV was chosen for our metric for phylogenetic diversity because it is statistically independent from species richness and any differences in PSV is due to abiotic conditions (Helmus *et al.* 2007, 2010). Therefore, PSR is a more accurate representation of phylogenetic diversity because the model incorporates the evolutionary divergence instead of using strictly Faith's PD. A paired t-test between urban and rural sites was used to determine if there were any differences in PSV, PSR, and SR.

A SURFACE analysis was used to determine the strength of urbanization as a selection pressure and identify clades that have similar optimal trait values (Ingram & Mahler 2013). This analysis determines if convergent evolution of a continuous trait occurs where multiple lineages have shifted to a mutual adaptive peak. SURFACE works through a forward, stepwise progression of Hansen models to identify regime shifts and then collapses regimes with similar optima in the backwards phase of the analysis. A regime shift is identified by trait optima (in this study, the trait proxy across *n* study sites) that reflect clades responding to urbanization in a similar way. Therefore, species can respond strongly positive or strongly negative to urbanization pressures and is visualized in the "preference" for one type of ecosystem or another.

CHAPTER 3
RESULTS

Meta-Analysis

Consistent with previous research, species richness was significantly lower in urbanized ecosystems than in rural ecosystems (mean ES = -0.514, $p < 0.001$). Overall, there were 15% fewer species in urban versus rural. In the traditional meta-analysis, 77% of the studies produced a negative effect size (lower biodiversity in urban ecosystems), while 22% of the studies produced a positive effect size (higher biodiversity in urban ecosystems). An analysis of publication bias across studies found that there is a bias towards publishing studies with results that indicate a decline in species diversity in urban ecosystems. However, after accounting for this bias using the trim and fill method, we still see a significant decrease in species richness in urbanized sites (mean ES = -0.276, $p = 0.019$). Kingdom was used as a moderator (Plant or Animal as factors) to address how much across study variation may be due to the natural history of the target communities. The results of this model suggest that both plant and animal diversity is significantly less in urban ecosystems than in rural ecosystems (Figure 1a-A, for all figures refer to Appendix II). The mean effect size of Plants was -0.369 ($p = 0.0014$) and the mean effect size of Animals was -0.8453 ($p < 0.0001$). Kingdom as a moderator accounted for 19% of the total variability within the overall effect size. In addition, we used growth type as a moderator and found that all growth forms except “Miscellaneous Plant” were statistically different from zero (Figure 1b, Table 1, for all tables refer to Appendix I). Growth form as a moderator also accounted for 19% of the total variability within the effect size; this is unsurprising since growth form is not independent from Kingdom.

Phylogenetic Analysis

Despite the strong effects of urbanization on species richness, there were no differences in PSV, PSR, and SR across the urbanization gradient (Figure 2, Table 2). The PSV value from the overall model for urban and rural sites was 0.35 and 0.35. The

PSR value from the overall model for urban and rural sites was 257.87 and 270.76. And the SR value from the overall model for urban and rural sites was 735 and 766, respectively. These results suggest that species communities in both urban and rural ecosystems are not very phylogenetically diverse. This pattern could be due to target taxa within studies (e.g. Burton et al. and trees), however more than half of the studies in this analysis incorporated surveys across broad taxonomical groups (i.e. not limited to only woody or only herbaceous plants).

Even though phylogenetic diversity did not differ between urban and rural sites, results from the SURFACE analysis indicate that urbanization is acting as a very strong selection pressure. The final Hansen model consisted of 10 regime shifts and a total of five distinct regimes (Figure 3, Table 3). AICc values improved from -45.80 to -139.816 (ΔAICc = 94.32) during the backward phase of the analysis (Figure 4, Table 3). There were a total of two convergent regimes and a total of three nonconvergent regimes. Collapsed regimes c and f (approximately 300 species) had positive trait optima indicating that the species within these regimes prefer rural ecosystems and will likely struggle in more urbanized ecosystems. Conversely, collapsed regimes b and d (16 species) strongly prefer urban ecosystems. The strength of selection was very large ($\alpha >> 20$) and phylogenetic half-life was small ($t_{1/2} = 0.0009$), implying that there is very fast movement toward an adaptive optimum trait value (θ) (Table 4). These results show that the groups of species that were collapsed into similar regimes possess functional traits that allow them to persist in either urban or rural ecosystems, suggesting that urbanization is acting as a force of natural selection.

CHAPTER 4
DISCUSSION

Rates of urbanization and habitat loss are predicted to be severe and are expected to influence global biodiversity patterns (Pimm & Raven 2000; McKinney 2006; Grimm *et al.* 2008). Consistent with previous research (Newbold *et al.* 2015), the results of this study show that urbanization has an overall negative effect on global biodiversity. Various growth forms within plants and animals show significant decreases in species richness within urban communities. Vertebrates in particular are affected more so by urbanization than invertebrates, while woody and herbaceous plant species have a similar negative response. These patterns are not surprising given urban ecosystems are extreme, containing several niches to which many species are not well adapted (Sattler *et al.* 2010). Such a strong selective filter results in communities that tend to have lower species diversity, but retain species that are more stress tolerant (Chase 2007). For example, opportunist animals, weedy plants, and invasive species are likely candidates to do well in harsh, disturbed environments (Kowarik 2008). Urbanization and the associated landscape modification may ultimately alter future patterns of biodiversity in favor of these species and their respective evolutionary lineages.

Consistent with the hypothesis that urbanization may drive patterns of diversity in the future, the results of this study show that urbanization is a very strong environmental filter that is promoting natural selection. While species richness is lower in urban environments, there is no difference in Phylogenetic Species Variance, Phylogenetic Species Richness, and Species Richness between urban and rural ecosystems, demonstrating that the mean diversity of evolutionary lineages in urban and rural communities is similar. Combined with the SURFACE analysis, these results indicate that whole evolutionary lineages are being filtered along the urbanization gradient. Additionally, the SURFACE analysis indicates that clades in urban environments are rapidly moving to new trait optima that allow particular groups of related species to persist in urban environments. For example, there are three convergent regimes

(Regimes 2, 8, and 9) that indicate movement toward a negative θ value (preference for urban ecosystems). These regimes consist of clades of plants that are ornamental as well as highly advantageous like *Poa compressa*, a dominant plant in its native range and invasive in its introduced range. Alternatively, there are four convergent regimes (Regimes 3, 5, 7, 10) that indicate movement towards a positive θ value (preference for rural ecosystems); these clades contain plants that are prominent meadow and forest species like herbaceous flowers and oak trees. In addition, one nonconvergent regime (Regime 6) indicated a weak movement toward a positive θ value, but remains close to zero. This regime contains approximately 300 species with 30% of the total species belonging to the family Asteraceae (asters) and 11% of species belonging to Laminaceae (mints). This suggests that the plants within this regime are capable of surviving in urban and rural ecosystems and the interspace in between, with a slight preference for rural environments. It is clear that urbanization is a powerful force and the strength of selection is exceptionally large; by comparison, urbanization is 4 x's stronger than pollinator-based selection (Anderson *et al.* 2014), nearly 250 x's stronger than herbivory-based selection (Turcotte *et al.* 2014), and 5-144 x's stronger than climate change based selection (68-144 x's stronger than temperature and 5-19 x's stronger than precipitation, depedning on the Ornstein-Uhlenbeck model used; Ren *et al.* 2015). The strong selective effects of urbanization and the shift to new trait optima along the urbanization gradient imply that some evolutionary lineages are more threatened by urbanization than others. This is an important result that suggests that, as a consequence of urbanization, whole related clades may be lost.

The idea that whole clades may be endangered should stimulate conversation around conservation efforts that focus on protecting evolutionary lineages. Traditional conservation strategies attempt to increase the amount of intact habitat by acquiring large parcels of land and expand the connectivity between patches (Lindenmayer *et al.* 2006). This method integrates natural areas into the urban infrastructure during the process of city planning and beautification; however, this approach neglects to incorporate long-term ramifications of urbanization as an evolutionary force. Because

urban centers are expected to intensify as a function of human population growth, evolutionary lineages that respond negatively to urbanization are likely to come under increasing threat. It is important that we address this issue because the loss of threatened clades will further homogenize the urban landscape and undermine ecosystem function (Winter *et al.* 2009). There have been many calls from the academic community to incorporate phylogenetic diversity into traditional biodiversity conservation plans (Faith 1992; Crozier 1997). However this has been met with resistance due to the lack of public appeal; phylogenetic diversity is seen as less important than focusing on endemic or threatened species (Mace 2003). This study reveals that there are threatened clades and that while phylogenetic diversity is not the focus *per se*, the concepts behind preserving evolutionary lineages will be paramount in contemporary conservation genetics efforts. There are two ways in which we can modify conservation efforts to reflect phylogenetic dynamics: (1) on a local scale and (2) on a broad scale. Methods outlined by Isaac *et al.* (2007) suggest that using comprehensive phylogenies that incorporates phylogenetic diversity and extinction risk can help identify clades that will need priority attention. In addition, other studies have used combinations of museum specimens and molecular genetics to determine the threat status of different taxonomic groups (Crandall *et al.* 2009). Both of these methods can be incorporated into local scale diversity assessments within cities and used to identify evolutionary lineages that may be particularly at risk. Using the information gained in local surveys we can infer phylogenetic information on a broad level by incorporating language in existing legislation that would emphasize the need to protect endangered clades. This two-step approach towards conserving biodiversity on the species and clade level will mitigate the impact that urbanization has on actively selecting against groups of species that are crucial for maintaining ecosystem function, thereby increasing integrity of the landscape.

In summary, this work quantified the strength of urbanization as an evolutionary force and identified distinctive regime shifts moving toward adaptive optima favoring either urban or rural environments. The results of this study imply that urbanization is

threatening the evolutionary trajectories of natural ecosystems, therefore we emphasize the need to incorporate phylogenetic inferences into existing conservation strategies. Urbanization transcends multiple ecosystems and creates an adaptive landscape where there will be very few winners unless further action is taken. Therefore, this work provides a foundation for studying urban ecology within the context of evolution.

REFERENCES

1.
Adler, P., Salguero-Gómez, R., Compagnoni, A., Hsu, J., Ray-Mukherjee, J., Mbeau-Ache, C., *et al.* (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, 111.

2.
Alberti, M. (2005). The effects of urban patterns on ecosystem function. *International regional science review*.

3.
Alexandratos, N. & Bruinsma, J. (2012). *World agriculture towards 2030/2050: the 2012 revision* (No. 12-03). FAO, Rome.

4.
Anderson, B, Ros, P & Wiese, TJ. (2014). Intraspecific divergence and convergence of floral tube length in specialized pollination interactions. *… of the Royal …*.

5.
Cadotte, M., Cavender-Bares, J., Tilman, D. & Oakley, T. (2009). Using Phylogenetic, Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. *PLoS ONE*, 4.

6.
Cavender- Bares, J, Kozak, KH & Fine, P. (2009). The merging of community ecology and phylogenetic biology. *Ecology …*.

7.
Charney, N & Record, S. (2013). Jost diversity measures for community data. *Package "vegetarian." Amherst*.

8.
Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. U.S.A.*, 104, 17430–4.

9.
Crandall, KA, Robison, HW & Buhay, JE. (2009). Avoidance of extinction through nonexistence: the use of museum specimens and molecular genetics to determine the taxonomic status of an endangered freshwater …. *Conservation Genetics*.

10.
Crozier. (1997). Preserving the Information Content of Species: Genetic Diversity, Phylogeny, and Conservation Worth. *Annual Review of Ecology and Systematics*, 28, 243–268.

11.

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.

12.
Faith, D. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.

13.
Grimm, NB, Faeth, SH, Golubiewski, NE & Redman, CL. (2008). Global change and the ecology of cities. *science*.

14.
Harmon, LJ, Weir, JT, Brock, CD & Glor, RE. (2008). GEIGER: investigating evolutionary radiations. ….

15.
Helmus, MR, Keller, WB, Paterson, MJ & Yan, ND. (2010). Communities contain closely related species during ecosystem disturbance. *Ecology* ….

16.
Helmus, MR, Savage, K, Diebel, MW & Maxted, JT. (2007). Separating the determinants of phylogenetic community structure. *Ecology* ….

17.
Ingram, T & Mahler, DL. (2013). SURFACE: detecting convergent evolution from comparative data by fitting Ornstein- Uhlenbeck models with stepwise Akaike Information Criterion. *Methods in Ecology and Evolution*.

18.
Isaac, N., Turvey, ST, Collen, B & Waterman, C. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One*.

19.
Kaye, J., Groffman, P., Grimm, N., Baker, L. & Pouyat, R. (2006). A distinct urban biogeochemistry? *Trends in Ecology & Evolution*.

20.
Kembel, SW, Cowan, PD & Helmus, MR. (2010). Picante: R tools for integrating phylogenies and ecology. ….

21.
Kowarik, I. (2008). On the role of alien species in urban flora and vegetation. *Urban ecology*.

22.

Lindenmayer, DB, Franklin, JF & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological conservation*.

23.
Liu, Z., He, C., Zhou, Y. & Wu, J. (2014). How much of the world's land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecol*, 29, 763–771.

24.
Mace. (2003). Preserving the Tree of Life. *Science*, 300, 1707–1709.

25.
McDonnell, MJ, Pickett, S., Groffman, P & Bohlen, P. (1997). Ecosystem processes along an urban-to-rural gradient. *… Ecosystems*.

26.
McDonnell, MJ, Pickett, S. & Pouyat, RV. (1993). The application of the ecological gradient paradigm to the study of urban effects. *… as components of ecosystems*.

27.
McKinney, ML. (2006). Urbanization as a major cause of biotic homogenization. *Biological conservation*.

28.
McKinney, ML. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban ecosystems*.

29.
Newbold, T., Hudson, L., Hill, S., Contu, S., Lysenko, I., Senior, R., *et al.* (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

30.
Paradis, E, Claude, J & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*.

31.
Pataki, DE, Alig, RJ & Fung, AS. (2006). Urban ecosystems and the North American carbon cycle. *Global Change …*.

32.
Paul, MJ & Meyer, JL. (2001). Streams in the urban landscape. *Annual Review of Ecology and Systematics*.

33.

Pickett, S., Cadenasso, ML, Grove, JM & Nilon, CH. (2008). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Urban Ecology*.

34.
Pimm, S. (2008). Biodiversity: Climate Change or Habitat Loss — Which Will Kill More Species? *Current Biology*, 18, R117–R119.

35.
Pimm, S. & Raven, P. (2000). Biodiversity: Extinction by numbers. *Nat.*, 403.

36.
Ren, G., Conti, E. & Salamin, N. (2015). Phylogeny and biogeography of Primula sect. Armerina: implications for plant evolution under climate change and the uplift of the Qinghai-Tibet Plateau. *BMC Evolutionary Biology*, 15.

37.
Revell, LJ. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*.

38.
Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M., *et al.* (2010). Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology*, 91.

39.
Turcotte, M.M., Davies, J.T., Thomsen, C.J. & Johnson, M.T. (2014). Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20140555.

40.
United Nations. (2015a). *World Urbanization Prospects: The 2014 Revision* (No. ST/ESA/SER.A/366). Department of Economic and Social Affairs, Population Division .

41.
United Nations. (2015b). *World Population Prospects: The 2015 Revision, Key Findings and Advance Tables* (No. No. ESA/P/WP.241). Department of Economic and Social Affairs, Population Division .

42.
Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*.

43.
Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W.,

et al. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, 7, 737–750.

44.
Webb, CO, Ackerly, DD & McPeek, MA. (2002). Phylogenies and community ecology. *Annual review of ecology* ….

45.
Williams, N., Schwartz, MW & Vesk, PA. (2009). A conceptual framework for predicting the effects of urban environments on floras. *Journal of* ….

46.
Winter, M, Schweiger, O & Klotz, S. (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the* ….

47.
Zanne, A., Tank, D., Cornwell, W., Eastman, J., Smith, S., FitzJohn, R., *et al.* (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92.

APPENDICES

APPENDIX I

TABLES

Table 1. Meta-Analysis moderators.

Significant factors are indicated with an asterisk.

Moderator	Factor	Estimate	p-value	Upper CI	Lower CI
Kingdom	Plant *	-0.3629	0.0014	-0.562	-0.1396
	Animal *	-0.8453	<0.0001	-1.1482	-0.5424
Growth Type	Herbaceous *	-0.5086	0.0468	-1.01	-0.0072
	Woody *	-0.4806	0.005	-0.8164	-0.1449
	Misc.	-0.1452	0.4595	-0.53	0.2394
	Vertebrate *	-1.8462	<0.0001	-2.6235	-1.0689
	Invertebrate *	-0.6488	0.0002	-0.9876	-0.31

Table 2. Phylogenetic Species Variance (PSV), Phylogenetic Species Richness (PSR), and Species Richness (SR) in Rural and Urban sites from each study

Mean PSV, PSR, and SR are pooled across studies for each site (± SE).

	Rural			Urban		
Study	**PSV**	**PSR**	**SR**	**PSV**	**PSR**	**SR**
Albrecht 2013	0.36	4.30	12	0.25	1.01	4
Burton 2008	0.39	20.86	54	0.40	16.76	42
Giordano 2004	0.54	2.72	5	0.70	3.52	5
Knapp 2008	0.34	188.94	560	0.34	179.82	530
Loewenstein 2005	0.42	25.50	61	0.37	20.36	55
Meek 2010	0.46	29.16	63	0.40	48.53	122
Rija 2014	0.39	20.52	52	0.40	14.43	36
Mean ± SE	0.41 ± 0.26	41.71 ± 23.83	115.28 ± 74.65	0.41 ± 0.52	40.63 ± 23.93	113 ± 71.02

Table 3. SURFACE analysis output.

Optima trait values (θ) are shown for the forward phase model and backward phase (collapsed), AIC scores and log-likelihood values for each regime shift are shown after backwards phase. Similar letters show collapse of regime shifts during the backwards phase of the analysis.

Regime Sequence	Forward Regimes	θ	AIC	log-likelihood	Regime Shifts	Collapsed Regimes	θ
1	a	0.0094	-45.497	26.766	a	a	0.009
2	b	-0.716	-61.528	36.806	b	b	-0.64
3	c	1	-75.060	45.603	c	c	0.852
4	d	-0.226	-84.268	52.245	d	d	-0.226
5	e	0.857	-93.297	58.806	c	f	0.065
6	f	0.065	-102.396	65.411	f	-	-
7	g	0.833	-111.596	72.074	c	-	-
8	h	-0.75	-118.867	77.782	b	-	-
9	i	-0.508	-125.482	83.170	b	-	-
10	j	0.7166	-131.421	88.228	c	-	-
11	-	-	-139.816	87.219	-	-	-

Table 4. SURFACE summary results.

The parameters in the table are defined as followed: α is the rate of adaptation to the optima, $\alpha_{1/2}$ is the expected half-life of α (the time to evolve halfway to an optimum), and σ^2 is the rate of stochastic evolution. Δk is the difference in the number of total number of regimes (k) and the total number of distinct regimes (k') after collapsing regimes in the backward phase of the analysis. c shows the number of convergent regime shifts that are occupied by multiple lineages. k'_{con} is the number of convergent regimes reached by multiple shifts and k'_{noncon} is the number of non-convergent regimes reached by multiple shifts.

α	$t_{1/2}$	σ^2	k	k'	Δk	c	K'_{con}	K'_{noncon}
753.95	0.0009	74.17	10	5	5	7	2	3

APPENDIX II

FIGURES

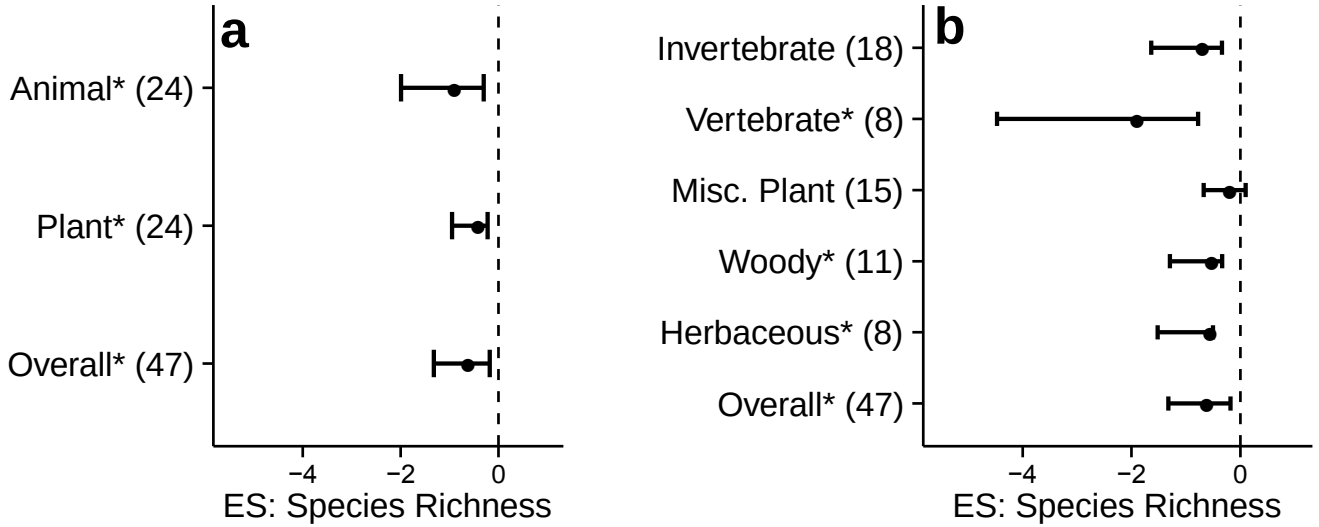

Figure 1-A Effect size of species richness for kingdom level moderators
Figure 1-B Effect size of species richness for growth form level moderators.

Negative effect size indicates lower richness in urban environments. Bars represent 95% confidence intervals. Effect size for each moderator is significant if confidence intervals do not overlap with zero (indicated by asterisk). Number of studies per moderator is shown in parentheses.

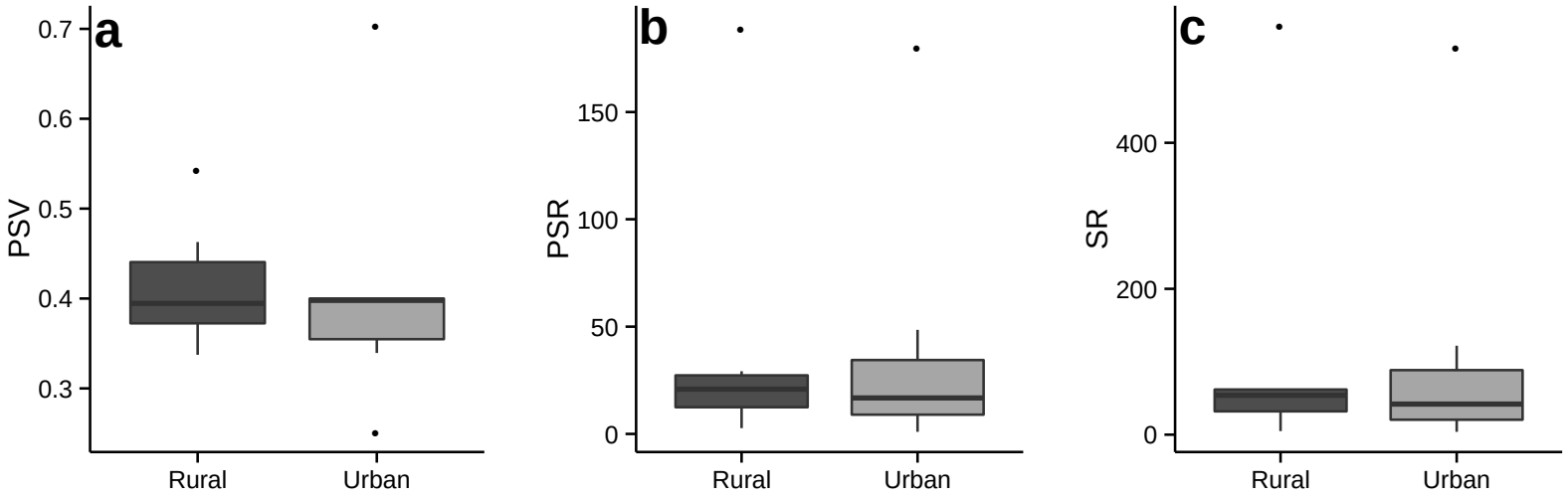

Figure 2-A. Phylogenetic Species Variance shown (PSV) in rural and urban communities.
Figure 2-B. Phylogenetic Species Richness (PSR) in rural and urban communities.
Figure 2-C. Species Richness (SR) in rural and urban communities.

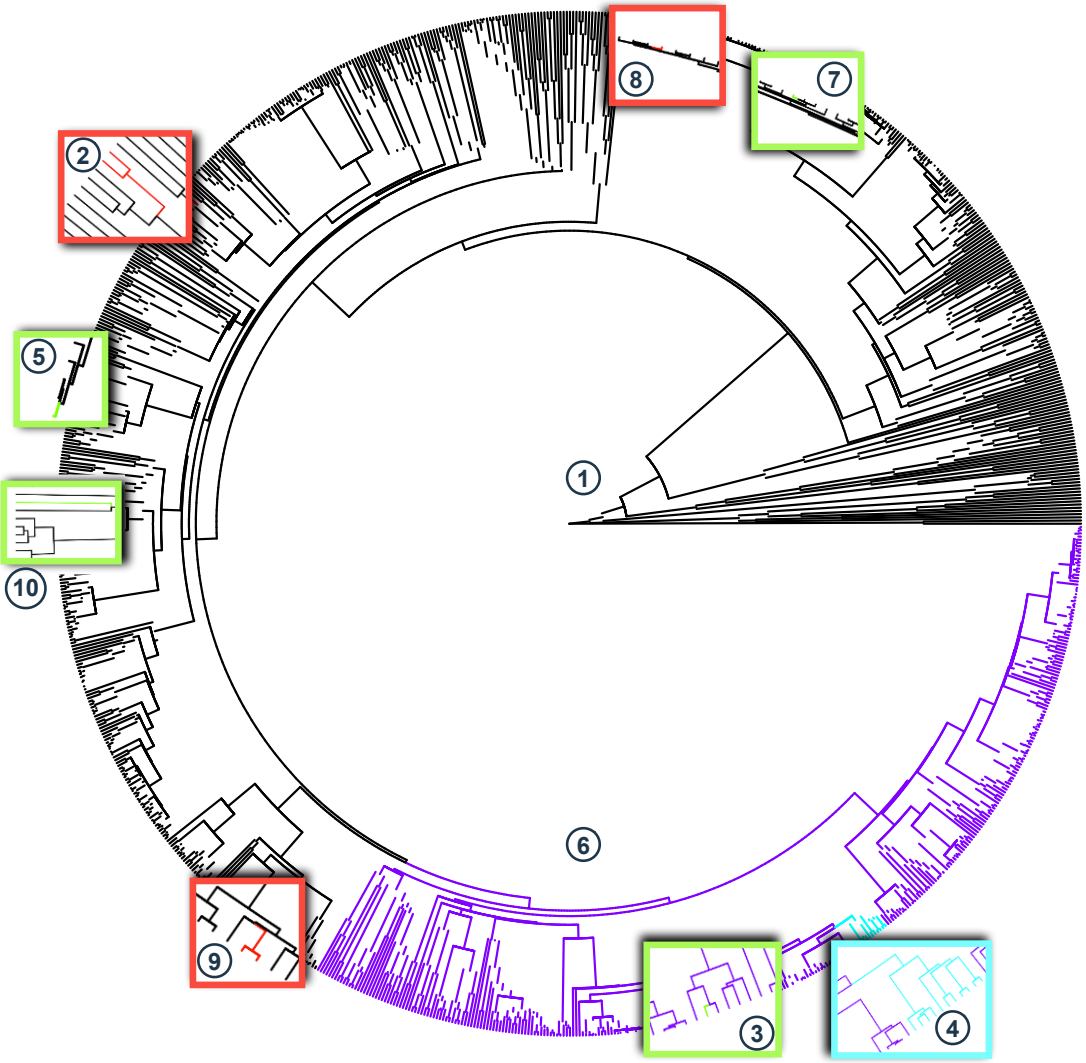

Figure 3. SURFACE Tree Output

Phylogenetic tree with different regime shifts. Numbers on the tree indicate the order in which regimes were added during the forward phase of the analysis. Red boxes show convergent clades that perform better in urban ecosystems. Green boxes show convergent clades that perform better in rural ecosystems. Convergent clades were identified in the backwards phase. Purple clade represents ~300 species that perform slightly better in rural ecosystems. Blue clade represents group of species that perform very well in urban environments. Regime 1 consists of the base tree.

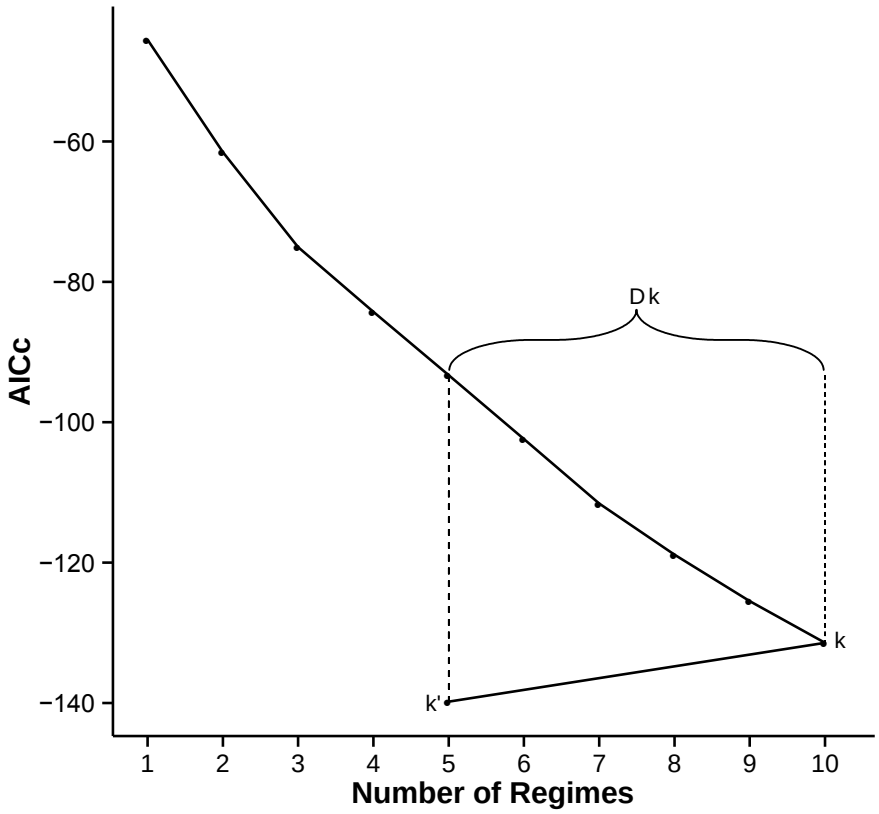

Figure 4. Change in AIC between the forwards and backwards phase of the SURFACE analysis.

Each forward step improved the overall model. The backward phase indicates further model improvement as regimes were collapsed, detecting convergent clades.

APPENDIX III

STUDIES USED IN META-ANALYSIS

1.
Albrecht, H. & Haider, S. (2013). Species diversity and life history traits in calcareous grasslands vary along an urbanization gradient. *Biodivers. Conservation*.

2.
Banville, M. & Bateman, H. (2012). Urban and wildland herpetofauna communities and riparian microhabitats along the Salt River, Arizona. *Urban Ecosyst.*, 15, 473–488.

3.
Barrett, MA & Stiling, P. (2006). Key deer impacts on hardwood hammocks near urban areas. *Journal of Wildlife Management*.

4.
Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J. & Hale, J.D. (2011). Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS ONE*, 6, 1–11.

5.
Bradley, C., Gibbs, S. & Altizer, S. (2008). Urban land use predicts West Nile virus exposure in songbirds. *Ecological Applications*, 18.

6.
Buczkowski, G. & Richmond, D.S. (2012). The Effect of Urbanization on Ant Abundance and Diversity: A Temporal Examination of Factors Affecting Biodiversity. *PLoS ONE*, 7, 1–9.

7.
Burton, M., Samuelson, L. & Mackenzie, M. (2009). Riparian woody plant traits across an urban–rural land use gradient and implications for watershed function with urbanization. *Landsc. Urban Plan.*, 90, 42–55.

8.
Chapman, K. & Reich, P. (2007). Land use and habitat gradients determine bird community diversity and abundance in suburban, rural and reserve landscapes of Minnesota, USA. *Biological Conservation*, 135, 527–541.

9.
Clergeau, P., Savard, J.-P., Mennechez, G. & Falardeau, G. (1998). Bird Abundance and Diversity along an Urban-Rural Gradient: A Comparative Study between Two Cities on Different Continents. *Condor*, 100.

10.

Desales-Lara, M., Francke, O. & Sánchez-Nava, P. (2013). Diversidad de arañas (Arachnida: Araneae) en hábitats antropogénicos. *Revista Mexicana De Biodiversidad*, 84, 291–305.

11.
Ehrenfeld, J. (2005). Vegetation of forested wetlands in urban and suburban landscapes in New Jersey1. *J. Torrey Botanical Soc.*, 141.

12.
Elek, Z. & Lövei, G. (2007). Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*, 32, 104–111.

13.
Gagné, S. & Fahrig, L. (2011). Do birds and beetles show similar responses to urbanization? *Ecol. Appl.*, 21.

14.
Giordano, S., Sorbo, S., Adamo, P., Basile, A., Spagnuolo, V. & Cobianchi, R. (2004). Biodiversity and trace element content of epiphytic bryophytes in urban and extraurban sites of southern Italy. *Plant Ecol.*, 170, 1–14.

15.
Gottschalk, M., Toni, D., Valente, V. & Hofmann, P. (2007). Changes in Brazilian Drosophilidae (Diptera) assemblages across an urbanisation gradient. *Neotropical Entomology*, 36, 848–862.

16.
Hope, D., Gries, C., Zhu, W., Fagan, W., Redman, C., Grimm, N., *et al.* (2003). Socioeconomics drive urban plant diversity. *Proc. Natl. Acad. Sci. United States Am.*, 100, 8788–92.

17.
Huang, L., Zhu, W., Ren, H., Chen, H. & Wang, J. (2012). Impact of atmospheric nitrogen deposition on soil properties and herb-layer diversity in remnant forests along an urban–rural gradient in Guangzhou, southern China. *Plant Ecol.*, 213, 1187–1202.

18.
Julião, G., Fernandes, G., Negreiros, D., Bedê, L. & Araújo, R. (2005). Insetos galhadores associados a duas espécies de plantas invasoras de áreas urbanas e peri-urbanas. *Revista Brasileira De Entomologia*, 49, 97–106.

19.
Kaltsas, D., Panayiotou, E., Chatzaki, M. & Mylonas, M. (2014). Ground spider assemblages (Araneae: Gnaphosidae) along an urban-rural gradient in the city of

Heraklion, Greece. *European Journal of Entomology*, 111, 59–67.

20.
Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008). Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol. Lett.*, 11, 1054–1064.

21.
Loewenstein, N. & Loewenstein, E. (2005). Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. *Urban Ecosyst.*, 8, 79–91.

22.
MacGregor-Fors, I., Avendaño-Reyes, S., Bandala, V., Chacón-Zapata, S., Díaz-Toribio, M., González-García, F., *et al.* (2014). Multi-taxonomic diversity patterns in a neotropical green city: a rapid biological assessment. *Urban Ecosyst.*, 18.

23.
Magura, T., Nagy, D. & Tóthmérész, B. (2013). Rove beetles respond heterogeneously to urbanization. *J. Insect Conservation*, 17, 715–724.

24.
Martin, S. & Lutterschmidt, W. (2013). A Checklist to the Common Cyprinid and Centrarchid Fishes of the Bull and Upatoi Creeks Watershed of Georgia with a Brief Glimpse of Correlative Urban Influences and Land use. *Southeast. Nat.*, 13.

25.
Meek, C., Richardson, D. & Mucina, L. (2010). A river runs through it: Land-use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa. *Biological Conservation*, 143, 156–164.

26.
Moffatt, S.F., McLachlan, S.M. & Kenkel, N.C. (2004). Impacts of land use on riparian forest along an urban – rural gradient in southern Manitoba. *Plant Ecol.*, 174, 119–135.

27.
Niemelä, J. & Kotze, D. (2009). Carabid beetle assemblages along urban to rural gradients: A review. *Landsc. Urban Plan.*, 92, 65–71.

28.
Nock, C., Paquette, A., Follett, M., Nowak, D. & Messier, C. (2013). Effects of Urbanization on Tree Species Functional Diversity in Eastern North America. *Ecosyst.*, 16.

29.
Van Nuland, M. & Whitlow, W. (2014). Temporal effects on biodiversity and composition

of arthropod communities along an urban–rural gradient. *Urban Ecosystems*, 17, 1047–1060.

30.
Oduola, A., Olojede, J., Oyewole, I., Otubanjo, O. & Awolola, T. (2013). Abundance and diversity of Anopheles species (Diptera: Culicidae) associated with malaria transmission in human dwellings in rural and urban communities in Oyo State, Southwestern Nigeria. *Parasitol. Res.*, 112.

31.
Porter, E., Forschner, B. & Blair, R. (2001). Woody vegetation and canopy fragmentation along a forest-to-urban gradient. *Urban Ecosyst.*, 5, 131–151.

32.
Riem, J., Blair, R., Pennington, D. & Solomon, N. (2012). Estimating Mammalian Species Diversity across an Urban Gradient. *Am. Midl. Nat.*, 172.

33.
Rija, A., Said, A., Mwamende, K., Hassan, S. & Madoffe, S. (2014). Urban sprawl and species movement may decimate natural plant diversity in an Afro-tropical city. *Biodivers. Conservation*, 23, 963–978.

34.
Sadler, J., Small, E., Fiszpan, H., Telfer, M. & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *J. Biogeography*, 33, 1126–1138.

35.
Silva, F. & Carvalho, L.P.C. (2013). A Population Study of the Culicoides Biting Midges (Diptera: Ceratopogonidae) in Urban, Rural, and Forested Sites in a Cerrado Area of Northeastern Brazil. *J. Comp. Neurology*, 107.

36.
Stapanian, M., Cassell, D. & Cline, S. (1997). Regional patterns of local diversity of trees: associations with anthropogenic disturbance. *For. Ecol. Management*, 93, 33–44.

37.
Tarvainen, O., Markkola, A. & Strömmer, R. (2003). Diversity of macrofungi and plants in Scots pine forests along an urban pollution gradient. *Basic Appl. Ecol.*, 4, 547–556.

38.
Thompson, K., Austin, K.C., Smith, R.M., Warren, P.H., Angold, P.G. & Gaston, K.J. (2003). Urban Domestic Gardens (I): Putting Small-Scale Plant Diversity in Context . *Journal of Vegetation Science*, 14, 71–78.

39.
Tian, Z., Song, K. & Da, L. (2015). Distribution patterns and traits of weed communities along an urban–rural gradient under rapid urbanization in Shanghai, China. *Weed Biology Management*, 15, 27–41.

40.
Turner, K, Lefler, L & Freedman, B. (2005). Plant communities of selected urbanized areas of Halifax, Nova Scotia, Canada. *Landscape and Urban Planning*.

41.
Vakhlamova, T., Rusterholz, H.-P., Kanibolotskaya, Y. & Baur, B. (2014). Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia. *Landsc. Urban Plan.*, 132.

42.
Vanbergen, A., Woodcock, B., Watt, A. & Niemelä, J. (2005). Effect of land- use heterogeneity on carabid communities at the landscape scale. *Ecography*, 28, 3–16.

43.
Verboven, H., Uyttenbroeck, R., Brys, R. & Hermy, M. (2014). Different responses of bees and hoverflies to land use in an urban–rural gradient show the importance of the nature of the rural land use. *Landsc. Urban Plan.*, 126, 31–41.

44.
Vilisics, F., Elek, Z., Lövei, G. & Hornung, E. (2007). Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark. *Pedobiologia*, 51, 45–53.

45.
Van der Walt, L., Cilliers, S.S., Toit, M.J. & Kellner, K. (2014). Conservation of fragmented grasslands as part of the urban green infrastructure: how important are species diversity, functional diversity and landscape functionality? *Urban Ecosystems*, 18, 87–113.

46.
Wang, Y., Meng, D., Zhu, Y. & Zhang, F. (2009). Impacts of regional urbanization development on plant diversity within boundary of built-up areas of different settlement categories in Jinzhong Basin, China. *Landsc. Urban Plan.*, 91, 212–218.

47.
White, R., Carreiro, M. & Zipperer, W. (2014). Woody plant communities along urban, suburban, and rural streams in Louisville, Kentucky, USA. *Urban Ecosyst.*, 17, 1061–1094.

VITA

Lauren C. Breza received her Bachelor of Science degree at the University of Tennessee with a major in Biology and a concentration in Ecology and Evolutionary Biology in May 2011. The following year Ms. Breza worked as a post-bachelor intern at Oak Ridge National Laboratory (ORNL). After her internship at ORNL, she spent the summer of 2012 riding a bicycle across the United States of America from the outer banks of North Carolina to the Olympic Peninsula in Washington. Upon completion of her bike tour, Ms. Breza continued working within her field as a laboratory technician at the University of Tennessee. Ms. Breza entered the graduate program in Ecology and Evolutionary Biology at the University of Tennessee in the fall of 2013. In addition, Ms. Breza was a 2013 recipient of the National Science Foundation Graduate Research Fellowship Program pre-doc. In December 2015 she received her Master's degree at the University of Tennessee in Ecology and Evolutionary Biology. Ms. Breza will continue her academic studies at the University of New Hampshire were she has been accepted into the Natural Resources and Earth Systems Science Ph.D. program.